

1 **Biotic and abiotic factors modulating wild boar relative abundance in Atlantic**
2 **Spain**

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17

18 **Abstract**

19 The population dynamics of wild ungulates, particularly wild boar (*Sus scrofa*) are
20 modulated by biotic (e.g. predation) and abiotic (environmental) determinants. Iberian
21 wolf (*Canis lupus signatus*; hereafter wolf) is considered the main predator of wild
22 ungulates and wild boar is one of the most important components of its diet in Atlantic
23 Spain. Despite the evident potential interference of predation in the environmental
24 patterns of wild boar population abundance, studies including both predation and abiotic
25 factors are scarce. Here we tested the effects of predation and environmental
26 characteristics on wild boar relative abundance using spatially explicit predictive
27 models. Variation partitioning procedures were used to investigate the relative
28 importance of each factor and their overlaid effects. Wild boar relative abundance was
29 determined by hunting bag statistics, including hunting effort related-variables (in order
30 to avoid problems derived from modeling rates) as covariates, while wolf attacks to
31 livestock were considered as a proxy of wolf frequency in the drive. Our results
32 suggested that a great deal of the variability in wild boar abundance can be explained by
33 wolf relative abundance. The relevance of this factor can be explained by the high
34 predation rates of wolf on juvenile wild boar. According to previous knowledge on the
35 wild boar ecology, our results showed that the species abundance is positively
36 influenced by the percentage of surface occupied by mature forest and heather providing
37 high food diversity and refuge, but these environmental variables achieved a low
38 explanatory capacity in the models in relation to wolf frequency. The holistic approach
39 followed in this study was attended to open new perspectives for thinking on the wolf-
40 livestock conflict and to adequate wild boar management strategies taking into account
41 hunting interests and natural processes.

42 **Keywords:** *Canis lupus signatus*, habitat structure, land use, spatially explicit model,
43 *Sus scrofa*.

44 **Introduction**

45 Populations of wild ungulates in general and wild boar (*Sus scrofa*) in particular, have
46 been expanding during recent decades across Europe, both in density and in
47 geographical range (Saez- Royuela and Tellería 1986; Gortázar et al. 2000; Apollonio et
48 al. 2010). Interspecific relationships –including predation–, reproduction, environmental
49 characteristics and hunting, modulate wild ungulate population dynamics (Okarma
50 1995; Latham 1999; Acevedo et al. 2006; Apollonio et al. 2010; Fonseca et al. 2011;
51 Servanty et al. 2011; Keuling et al. 2013). Ungulates, whilst being major consumers of
52 vegetation, are themselves consumed by predators, revealing much about dominant
53 trophic linkages in terrestrial systems (Schmitz et al. 2000; Peterson 2003). Whereas the
54 actual dynamics of predator-ungulate interaction can be determined by preferred prey
55 species and predator abundance (Latham 1999; Nowak et al. 2005; Barja 2009; Davis et
56 al. 2012), the habitat-ungulate interaction is mainly determined by habitat composition
57 and structure (Abaigar et al. 1994). Thus, predator-related features and habitat
58 characteristics should be considered in unison when studying the population dynamics
59 of wild ungulates.

60 The wolf (*Canis lupus*) is usually considered the main predator of ungulates
61 (Jedrzejewski et al. 1992; Nowak et al. 2005; Valdmann et al. 2005). In fact, the wild
62 boar has been identified as the main food resource in the wolf diet in many studies in
63 Europe (e.g. Cuesta et al. 1991; Meriggi and Lovari 1996; Capitani et al. 2004; Nores et
64 al. 2008; Barja 2009; Wagner et al. 2012), reflecting the wolf's opportunist character,
65 preying on the more abundant preys (Glasser 1982; Salvador and Abad 1987), but in
66 other instances indicating sometimes the preference of wild boar (e.g. Fernández-Gil
67 2004; Davis et al. 2012). In this respect, Nores et al. (2008) estimated that wolf
68 predation causes 12% of wild boar mortality in Atlantic Spain. Thus, close relationships

69 between the population dynamics of both wolf and wild boar can be expected. For
70 instance, it has been found that when wolf populations decrease, wild boar populations
71 tend to increase (Sáez-Royuela and Tellería 1986; Gerard et al. 1991). But this is not an
72 inflexible rule since a limited effect of wolf numbers on wild boar populations has been
73 detected in other studies (e.g. Melis et al. 2006).

74 The association between wolf and wild ungulates may be an important piece for
75 mediating in the wolf-livestock conflict (Fritts and Mech 1981; Jhala 1993; Gazzola et
76 al. 2005; Nowak et al. 2005; Barja 2009; Hosseini-Zavarei et al. 2013). The abundance,
77 richness and diversity of wild ungulates is related to livestock consumption (Meriggi
78 and Lovari 1996), such that there is a reduction in wolf attacks on livestock in areas
79 where ungulates are abundant and diverse (see also Meriggi and Lovari 1996; Urios et
80 al. 2000; Sidorovich et al. 2003). At this level, ungulate abundance at large spatial
81 scales is modulated by habitat. The relationships between wild boar population
82 abundance and habitat characteristics, despite the generalist character of the species, are
83 well determined (Taylor et al. 1998; Cahill et al. 2003; Acevedo et al. 2006; Herrero et
84 al. 2006) and wild boar selects heterogeneous landscapes, dominated by mature forest,
85 that provide high food diversity and refuge (Abaigar et al. 1994; Fernández-Llario 2004;
86 Acevedo et al. 2006).

87 Data of wildlife population abundance is not easy to record for large spatial scales.
88 Thus, indirect methods are commonly used, in particular for elusive species such as
89 wild boar and/or wolf (reviewed by Llaneza et al. 1998; Engeman et al. 2013). For
90 instance, hunting bag derived-statistics are the most widely employed indirect indices to
91 determine wild boar relative abundances due to the method's low cost and simplicity,
92 and the feasibility of carrying out studies at large spatial-temporal scales (e.g. Sáez-
93 Royuela and Tellería 1986; Acevedo et al. 2006, 2011; Rodríguez-Prieto et al. 2012).

94 Despite their limitations, when hunting effort is taken into account, these indices
95 produce a reliable estimation of wild boar population abundance at both local and large
96 spatio-temporal scales (Acevedo et al. 2007; Imperio et al. 2010). Wolf abundance can
97 be estimated with direct methods rather than indirect ones or, indeed, with a
98 combination of both, the latter being highlighted by Llaneza et al. (1998) as the most
99 effective procedure. In addition, while it is true that more reliable estimates of wolf
100 abundance are obtained from direct methods, an index based on the number of livestock
101 attacks by wolves can be used to roughly estimate wolf relative abundance (Kusak et al.
102 2005; Hosseini-Zavarei et al. 2013), by considering the availability of livestock as the
103 most important factor determining wolf frequency (Uzal and Llaneza 2010; Eggerman
104 et al. 2011). Livestock attacks largely correspond to confirmed wolf presence (Pimenta
105 et al. 2005) and are considered a useful tool to assess the presence of dispersed
106 individuals, the emergence and establishment of the wolf in new areas, and also in
107 feeding studies (Dos Santos Reis and López 1997; Alexandre et al. 2000; Urios et al.
108 2000).

109 As previously stated, numerous studies have assessed the effects of predators or habitat
110 on wild boar abundance but, in contrast, studies that simultaneously include these two
111 factors are scarce (but see Melis et al. 2006). In this context, the aim of our study was
112 to, firstly, investigate the effects of habitat features which modulate the relative
113 abundance of wild boar populations and, secondly, how the abundance of boars is
114 related to frequency of wolf attacks in the area. The analysis of these complex systems
115 attempts to open up new perspectives for thinking about the wolf-livestock conflict (see
116 Treves et al. 2004).

117

118 **Materials and methods**

119 *Study area*

120 This study was conducted across Asturias, a province located in northwestern Spain,
121 during September-February 2007-2010. Specifically, data were collected in the
122 Regional Game Reserves (RGRs; Figure 1) located throughout the Cantabrian
123 Mountains, which include several protected areas and threatened and diverse fauna such
124 as Brown bear *Ursus arctos*, Cantabrian capercaillie *Tetrao urogallus* and Iberian wolf
125 *Canis lupus signatus* (hereafter wolf).

126 RGRs are characterized by an Atlantic climate. In medium elevation (500-1500 m)
127 areas, deciduous mixed forests are predominant with beech *Fagus sylvatica*, chestnut
128 *Castanea sativa*, oak *Quercus robur*, *Q. petraea*, *Q. pyrenaica*, *Q. orocantabrica*, holly
129 *Ilex aquifolium* and hazel *Corilus avellana*. However, higher areas (>1500 m) are
130 dominated by broom, scrub and heather: *Genista* spp., *Cytisus* spp., *Erica* spp., *Calluna*
131 spp., *Vaccinium* spp., *Juniperus* spp.

132

133 *Wild boar relative abundance index and hunting methodological variables*

134 To estimate wild boar abundance it is not an easy task. At large spatial-temporal scales
135 hunting bag statistics are the most recommendable, cost-effective and suitable option
136 (e.g. Boitani et al. 1995; Imperio et al. 2010), since the information is freely available at
137 no cost, and only requires the information to be registered and centralized on a database
138 (Sáez-Royuela and Tellería 1986; Acevedo et al. in press). Acevedo et al. (2009)
139 pointed out the importance of hunting effectiveness to estimate wild boar abundance by
140 using these kinds of indices, and they suggested that as effectiveness varied between
141 areas, more precise estimations can be obtained if the number of boars seen –instead of
142 the number of animals hunted– was considered. In this study the number of wild boar

143 seen in each battue was considered as our response variable. We obtained data from 704
144 battues during the 2007-2010 hunting seasons. Since the 2007/2008 hunting season, for
145 each wild boar battue the game wardens in the RGRs have systematically recorded
146 number of seen boars, hunting effort (number of hunters, beaters and dogs) and the
147 drive (our territorial sampling unit; Figure 1) in their activity reports. In the Cantabrian
148 Mountains, each battue is conducted on a given drive (n=268) –the small area of each
149 individual hunt–, which is within a hunting area (n=46), which is in turn part of an RGR
150 (n=11); in other words, an RGR contains several hunting areas and each one contains
151 several drives. RGRs, hunting areas and drives are georeferenced.

152 Our wild boar data represents raw information on the number of wild boars seen, i.e., it
153 is not standardized by sampling effort. Several studies have pointed out potential
154 problems associated with the use of ratios –as the standardized indices– when
155 performing statistical models and they suggest directly modeling the numerator as
156 response variable but including the denominator as covariate/s in the model (e.g.
157 Kronmal 1993). Thus, for modeling purposes we included variables accounting for
158 sampling effort and sampling period as covariates. These hunting methodological
159 variables were; total number of hunters, beaters and dogs (10-31), surface area of the
160 drive (range: 5-600 ha), and month (from September to February).

161

162 *Environmental characteristics: vegetation and topography*

163 For each drive we extracted environmental variables to be used as predictors of the
164 variations in wild boar relative abundance from the thematic regional cartography (GIS
165 of the Environmental Thematic Cartography, 1:25000 scaled, Environmental Agency of
166 Asturias, 1997). Seven different vegetation classes (quantified as percentage of surface

167 occupied by each class) were used as predictors in line with previous studies on the
168 environmental factors determining wild boar abundance (e.g. Acevedo et al. 2009, in
169 press): mature forest (mainly oak and beech), pre forest, broom and scrub, heather, tree
170 plantations, fern and meadows. In addition habitat diversity in each drive was calculated
171 using Shannon's diversity index (see McGarigal and Marks 1995). Finally, the
172 topographic data, average altitude (m a.s.l), average slope (percentage) and south-west
173 orientation (percentage of surface occupied by this orientation class; Fernández-Llario
174 2004; Acevedo et al. 2009) were extracted for each drive from a digital elevation model
175 grid (spatial resolution of 30 m; ASTER Global Digital Elevation Model V001)
176 (Japanese Ministry of Economy, Trade and Industry and N.A.S.A.).

177

178 *Wolf frequency*

179 In order to take into account the abundance of predator on wild boar-habitat
180 relationships, we included, as predictor, a proxy of wolf frequency in the drive; it being
181 the main wild predator of wild boar in Spain (Nores et al. 2008). Wolf frequency was
182 quantified from the livestock-attack reports of the Environmental Agency of Asturias
183 game wardens in the RGRs, a valuable tool to locate and identify individuals and
184 reproductive units, and as a proxy for describing their movements and territories (Dos
185 Santos Reis and López 1997; Alexandre et al. 2000). Particularly in Asturias, livestock-
186 attack data of wolf attacks to livestock are recognized as highly reliable (Talegon and
187 Gayol 2010). Each attack location was georeferenced and assigned to the drives within a
188 2.5 km radius, according to the wolf's area of activity (Ciucci et al., 1997; Jedrzejewski
189 et al. 2002; Kusak et al. 2005; Llaneza et al. 2011). Wolf frequency was calculated as
190 the sum of the wolf attacks on livestock per month during the hunting season

191 (September to February) (Kusak et al. 2005; Eggerman et al. 2011; Hosseini-Zavarei et
192 al. 2013).

193

194 *Statistical analysis*

195 To study the differential effects of habitat composition and structure, and wolf
196 frequency modulation on wild boar population abundance, we performed Generalized
197 Linear Mixed Models (GLMMs) with a Poisson distribution and logarithmic link
198 function. The most parsimonious models were selected using a backward stepwise
199 procedure based on Akaike Information Criteria (AIC; Akaike 1974). We considered
200 those models separated by less than 2 AIC points as having similar strength evidence
201 (Burnham and Anderson 2002). Territory (RGR, hunting area and drive, were all nested
202 and considered as a single variable) and hunting season was considered as random
203 factor. In addition, the methodological variables (period, surface area and hunting
204 effort), the environmental ones (habitat composition and structure) and wolf frequency
205 were considered as fixed factors. All statistical analyses were performed with the
206 software R 12.1 (R DevelopmentCore Team 2006), package 'lme4' (Bates et al. 2012).

207 Finally, to enhance the explanatory power of the models we performed variation
208 partitioning procedures (Borcard et al. 1992), in order to estimate the variation in the
209 final models which were independently explained by each factor (pure effects) and the
210 variation explained by two or more factors simultaneously (overlaid effects). It should
211 be noted that each factor is a group of related-predictors; in this study we took into
212 account three factors: methodology (Hm), environment (E) and wolf frequency (W).
213 After the development of the final models (Hm+E+W), we modeled our response
214 variable independently with variables related to each factor (Hm, E and W), as well as

215 with each pair of factors (Hm+E, Hm+W and E+W) to obtain the partial models. We
216 determined the variation explained by final and partial models in terms of explained
217 deviance. These amounts of variation were then used in R package modEva in order to
218 draw the diagram (Barbosa et al. 2013).

219

220 **Results**

221 Wild boar occurred in 85.2% of the drives, with numbers varying between 1 and 33
222 individuals seen per battue. Results of the four models separated by less than 2 AIC
223 points are reported in Table 1, and they share most of the significant predictors. The
224 explained deviance of the most parsimonious model was 10.76%; although the other
225 three models showed a similar degree of explained deviance (10.75-11.03%).

226 In the four models selected we found significant associations between wild boar
227 numbers and hunting methodological variables: period, surface area and hunting effort.

228 The number of wild boars seen was higher in bigger drives with a higher hunting effort.

229 In addition, the number of individuals seen increased during the period (highest in
230 February). After controlling for methodological factors, we found a positive relationship
231 between the surface area occupied by mature forest and heather and wild boar relative
232 abundance. Elevation was negatively related to the response variable, lower wild boar
233 relative abundance was observed in high elevation battues (in three of the four models).

234 Finally wolf attacks on livestock occurred in 57.5% of the drives, with between 1 and
235 28 attacks per battue during the hunting season. A positive association between the
236 relative abundance of wild boar and wolf attacks frequency was also detected in all four
237 models.

238 Results of variation partitioning in the four models showed that the pure effect of wolf
239 frequency explained the highest percentage of the explained deviance (65.4-67.5%)

240 followed by the pure effect of the methodological factor (21.1-22.6%). However, the
241 habitat factor only explained between 6.2 and 8.0% of deviance (see Figure 2 and
242 Appendix 2).

243

244 **Discussion**

245 This study evidences that a great deal of the variability in wild boar abundance,
246 estimated through hunting bags, can be explained by wolf frequency and that predation
247 was the main factor modulating wild boar population dynamics (Jedrzejewski et al.
248 1992; Mattioli et al. 1995; Kanzaki et al. 1998; Nores et al. 2008) followed by
249 environmental characteristics, this latter being considered in many studies as the unique
250 factor influencing distribution/abundance. The generalist character in habitat terms of
251 the target species may, at a certain level, account for the large amount of unexplained
252 deviance in our model, but is reasonable to assume that the potential effect of
253 uncontrolled environmental factors plays a part.

254

255 *On the methodological approach: hunting methodological variables*

256 The most widely employed method to estimate wild boar relative abundance is based on
257 hunting bag statistics standardized by hunting effort (see Sáez-Royuela and Tellería
258 1986; Acevedo et al. 2006, 2009, 2011; Engeman et al. 2013). These standardized
259 indices have been assessed both at local (Acevedo et al. 2007) and at large spatio-
260 temporal scales (Imperio et al. 2010; Acevedo et al. in press). Since there have been
261 criticisms of the use of ratios (e.g. Kronmal 1993), in this study hunting methodological
262 variables were included as covariates in the models rather than using only standardized
263 hunting bag data, and raw data of the number of wild boar seen during the drive was
264 used as response variable. This kind of analytical approach has recently been

265 highlighted in the context of body condition measures (Serrano et al. 2008; see also
266 Santos et al. 2013) and it has potential to be used in ecological modeling.

267

268 *Biotic interactions and abiotic requirements*

269 Many studies have attempted to determine the prey preference of wolves, and hence the
270 species more heavily influenced by wolf population dynamics (Nowak et al. 2005;
271 Eggerman et al. 2011; Wagner et al. 2012). Wolf preferential consumption of wild
272 ungulates, and especially of wild boar, has been reported in some regions of Europe
273 (Garzón-Heydt 1991; Rosell et al. 2001; Eggerman et al. 2011; Llana et al. 2011;
274 Davis et al. 2012) due to the higher abundance and availability of wild boar in the local
275 ungulate community (e.g. Jêdrzejewski et al. 2000) and to its increasing susceptibility in
276 winter seasons (Smietana and Klimek 1993). In NW Spain wild boar and roe deer
277 (*Capreolus capreolus*) are the main wild prey of wolves and their consumption
278 increases during the birthing season, probably because of the higher vulnerability of
279 newly born animals (Cuesta et al. 1991; Fernández-Gil 2004; Markina 2005; Nores et
280 al. 2008; Barja 2009).

281 In our study, independent of environmental characteristics, wolf attacks and wild boar
282 abundance were positively associated during autumn and winter. This finding may
283 suggest that wolves are more frequent in areas where wild boar is locally abundant in
284 line with density-dependent food exploitation (e.g. Peckarsky et al. 2008). The strong
285 relationship between prey and predator population dynamics can be explained by the
286 high predation rates of wolf on juvenile wild boar (Mech 1970; Ballard et al. 1987;
287 Salvador and Abad 1987; Jêdrzejewski et al. 1992; Mattioli et al. 2004; Nores et al.
288 2008) bearing in mind the usual birthing period at the end of February may be
289 supplemented by a second in autumn if conditions are favorable for boars (e.g. Ruiz-
290 Fons et al. 2006). In contrast to our findings showing a positive association between

291 livestock attacks and wild boar abundance, some researchers indicate that attacks on
292 livestock are less frequent in areas where there are high densities of several wild species
293 for wolf to prey on (Meriggi and Lovari 1996; Urios et al. 2000; Sidorovich et al. 2003).
294 Wolf livestock selection in this case can be explained by the encounter rate with
295 livestock due to spatial-temporal overlap (Huggard 1993). Urios et al. (2000) found –
296 from November to February– an increase in livestock attacks due to the increased food
297 requirements of wolf juveniles and their first attempts to hunt easy prey. In addition,
298 both the generalized expansion of wild ungulates and the high adaptability of wild
299 ungulates to human-dominated landscapes have been reported as important factors
300 which facilitate the occurrence and persistence of large predators in anthropogenic areas
301 (e.g. Ensenrink and Vogel 2006; Basille et al. 2009; Mladenoff et al. 2009; Llaneza et
302 al. 2011), which may enhance human-wolf conflicts.

303 Generalist species like wild boar show wide ecological plasticity (Saez-Royuela and
304 Tellería 1986; Taylor et al. 1998) and this ecological trait may explain the low weight of
305 environmental characteristics in the modulation of wild boar abundance in our models.
306 Nevertheless, in accordance to previous knowledge on the ecology of the species, our
307 results show that the abundance of wild boar was positively influenced by the
308 percentage of surface occupied by mature forest (oak and beech) and heather (e.g.
309 Acevedo et al. 2006; 2009). The wild boar likely behaved according to the food
310 exploitation hypothesis, whereby they fed mainly on acorns in autumn and winter due to
311 them adapting to the local and seasonal availability of food (oak acorns, beechnuts and
312 pine needles in autumn and winter) in the Cantabrian Mountains (Santos et al. 2004;
313 Uzal and Nores 2004). Wild boar also selected lower or medium elevation areas during
314 the hunting season due to the absence of snow in these areas, the amount of food

315 resources in winter time (Acevedo et al. 2006) and wild boar nest construction at the
316 beginning of the birth peak in the final weeks of February (Fernández-Llario 2004).
317 Based on our findings, we suggest that the inclusion of wolf frequency alongside
318 environmental characteristics in the models increases their ability to explain wild boar
319 abundance and the precision of the weight assigned to each factor. Consequently, if
320 wolf frequency was not included in the models, a slight overestimation of the weight of
321 environmental factor may well be produced (Figure 2). Furthermore, the increase in
322 wild boar abundance in northern Spain (e.g. Uzal and Nores 2004), requires the
323 adoption of appropriate management strategies which pay attention to both hunting
324 interests and natural processes. The challenge remains to determine whether controlling
325 wildlife population effects will reduce wolf-human conflict or rather favor it, but here
326 we provide support for a close relationship between wild boar and wolf frequency.

327

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339

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560

561 Table 1. Results of generalized linear mixed models explaining variation in wild boar
 562 relative abundance. Only the best models (i.e. those with the lowest AIC) are shown.
 563 See Appendix 1 for the full list of models tested.

AIC: 2731

| Model Predictors | Estimate | SE | Z value | P |
|-------------------------|-----------------|-----------|----------------|----------|
| Surface Area | 0.2146 | 0.0583 | 3.675 | <0.001 |
| Period | 0.0775 | 0.0163 | 4.747 | <0.001 |
| Hunting effort | 0.0281 | 0.0074 | 3.786 | <0.001 |
| Elevation | -0.0005 | 0.0002 | -1.811 | <0.100 |
| Mature forest | 0.5699 | 0.2486 | 2.292 | <0.050 |
| Heather | 2.1344 | 0.5394 | 3.957 | <0.001 |
| Wolf frequency | 0.0678 | 0.0055 | 12.214 | <0.001 |

AIC: 2732

| Model Predictors | Estimate | SE | Z value | P |
|-------------------------|-----------------|-----------|----------------|----------|
| Surface Area | 0.2019 | 0.0600 | 3.361 | <0.001 |
| Period | 0.0771 | 0.1632 | 4.724 | <0.001 |
| Hunting effort | 0.0281 | 0.0074 | 3.802 | <0.001 |
| Elevation | -0.0004 | 0.0002 | -1.672 | <0.100 |
| Mature forest | 0.6100 | 0.2527 | 2.414 | <0.050 |
| Heather | 2.0988 | 0.5407 | 3.881 | <0.001 |
| Diversity | 0.1157 | 0.1215 | 0.952 | 0.341 |
| Wolf frequency | 0.0676 | 0.0055 | 12.18 | <0.001 |

AIC: 2732

| Model Predictors | Estimate | SE | Z value | P |
|-------------------------|-----------------|-----------|----------------|----------|
| Surface Area | 0.1886 | 0.0573 | 3.292 | <0.001 |
| Period | 0.0776 | 0.0163 | 4.755 | <0.001 |
| Hunting effort | 0.0274 | 0.0074 | 3.709 | <0.001 |
| Mature forest | 0.4468 | 0.2357 | 1.896 | <0.100 |
| Heather | 2.0284 | 0.5359 | 3.785 | <0.001 |
| Wolf frequency | 0.0681 | 0.0055 | 12.259 | <0.001 |

AIC:2733

| Model Predictors | Estimate | SE | Z value | P |
|-------------------------|-----------------|-----------|----------------|----------|
| Surface Area | 0.1925 | 0.0604 | 3.185 | <0.001 |
| Period | -0.0004 | 0.0003 | -1.533 | <0.001 |
| Hunting effort | 0.0280 | 0.0074 | 3.787 | <0.001 |
| Elevation | -0.0004 | 0.0003 | -1.533 | 0.125 |
| Mature forest | 0.5937 | 0.2525 | 2.351 | <0.05 |
| Heather | 2.0614 | 0.5402 | 3.816 | <0.001 |

| | | | | | |
|----------------|--|---------|--------|--------|--------|
| Diversity | | 0.1545 | 0.1287 | 1.200 | 0.230 |
| Fern | | -0.6190 | 0.6538 | -0.947 | 0.344 |
| Wolf frequency | | 0.0670 | 0.0055 | 12.185 | <0.001 |

564

565

566 **Figure captions**

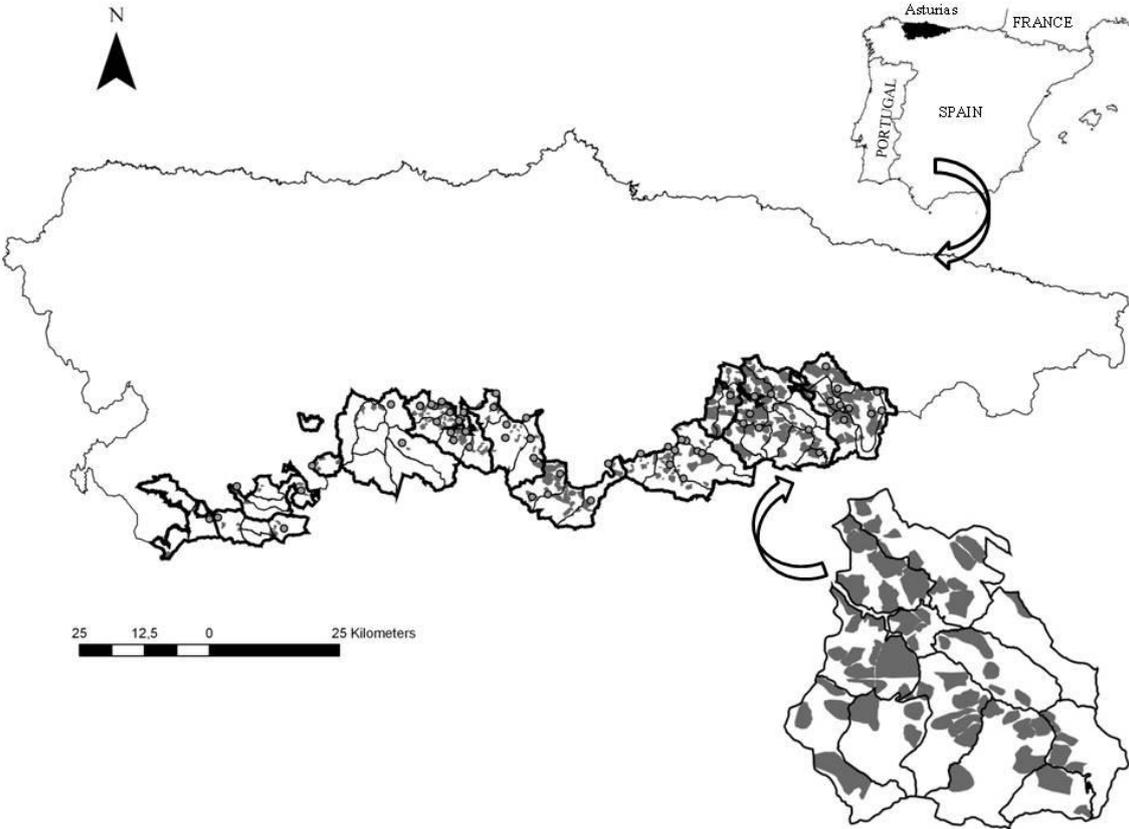
567 Figure 1. Geographical location of Asturias in Spain, location of study areas in the
568 Cantabrian Mountains (NW Spain) and detail for one RGR and its hunting areas and
569 drives. Polygons show Regional Game Reserves (RGRs, in bold black), hunting areas
570 (in black) and drives (grey areas) where data on wild boar abundance were obtained and
571 white circles show wolf attacks.

572 Figure 2. Variation partitioning results for the three factors retained in the most
573 parsimonious GLMM model including surface area, period and hunting effort as
574 hunting methodology factor; mature forest, heather and elevation as environment factor;
575 and wolf frequency.

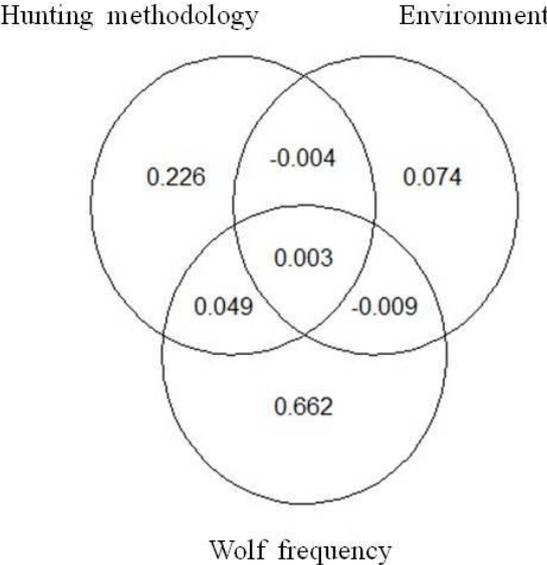
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577 Figure1

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Supplementary Material

583

584 **Biotic and abiotic factors modulating wild boar relative abundance in Atlantic**

585

Spain

586 Appendix 1. List of the 10 models tested per indicator group and their AIC values

587 following a backward stepwise process. The best models (separated by less than 2 AIC

588 points) are highlighted in bold.

589 A=surface area; P= period; He=hunting effort; E=elevation; S=slope; SW=southwest

590 orientation; Mf=mature forest; H=heather; F=fern; Pr=preforest; Sh=shrub; P=tree

591 plantation; M=meadows; D=vegetation diversity; W=wolf frequency

Variables

A+P+H e+E+M f+H+W

AIC

2731

A+P+H e+E+M F+H+D+W

2732

A+P+H e+MF+H+W

2732

A+P+H e+E+M f+H+F+D+W

2733

A+P+H e+E+M f+H+F+P+D+W

2734

A+P+H e+E+M f+Pr+H+F+P+D+W

2735

A+P+H e+S+E+M f+P+H+F+Ps+D+W

2737

A+P+H e+S+E+M f+Pr+H+F+P+M+D+W

2739

A+P+H e+S+E+M f+Pr+Sh+H+F+P+M+D+W

2741

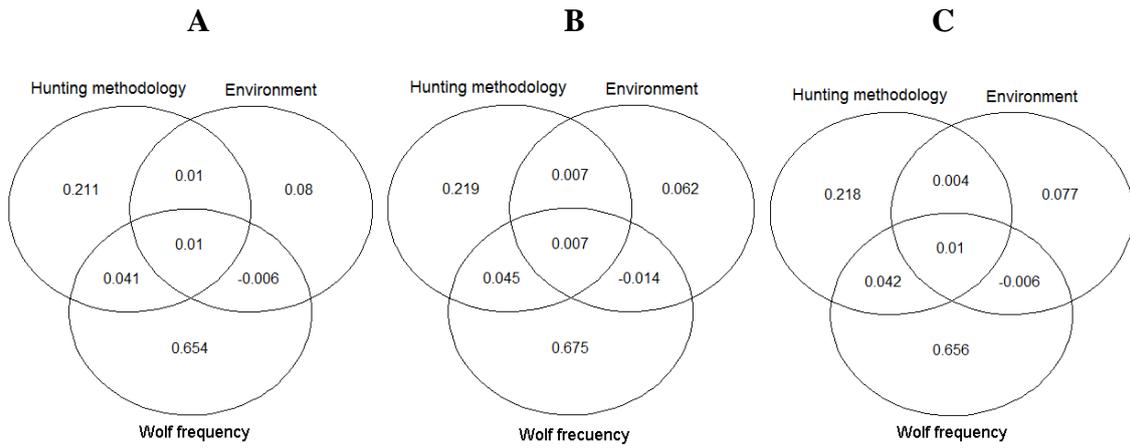
A+P+H e+S+E+SW+M f+Pr+Sh+H+F+P+M+D+W

2743

592

593 Appendix 2. Variation partitioning results for the three factors resulting from the three
 594 GLMM models: A, with AIC: 2732, which includes vegetation diversity; B, with AIC:
 595 2732, which excludes elevation; C, with AIC: 2733, which includes vegetation diversity
 596 and fern. In addition all include surface area, period and hunting effort as hunting
 597 methodology factor; mature forest, heather and elevation as environment factor; and
 598 wolf frequency.

599
 600



601